STUDIES ON THE DEEP SEA PROTOBRANCHIA; THE SUBFAMILY SPINULINAE (FAMILY NUCULANIDAE)

J. A. ALLEN[1]

H. L. SANDERS[2]

ABSTRACT. Species of the subgenera *Spinula* and *Bathyspinula* are combined within a new subfamily Spinulinae of the family Nuculanidae. Five species of the genus *Spinula* are described from the lower slope (500–2000 m) and abyss (2000–5000 m) of the Atlantic; four are new to the Atlantic, three are new to science, and one requires redescription. Detailed descriptions of their morphology are given and comparisons are made. It is suggested that the genus *Spinula* is a fast, subsurface burrower, capable of processing large amounts of sediment, and may be the abyssal counterpart of the shallow water Tellinacea. It is also suggested that, in association with the taking in of large quantities of sediment, these animals are modified to eject excessive amounts of pseudofaeces via the feeding aperture and with the aid of the posterior margin of the foot. This process may involve using the secretions of the 'byssal gland' as adhesive material to hold the flocculant waste together.

INTRODUCTION

In our first three papers in this series on the protobranchiate bivalves of the abyssal Atlantic (Sanders and Allen, 1973, 1977; Allen and Sanders, 1973) we investigated clearly defined groups which have characters that are in many ways extreme in form relative to the majority of the species of the Protobranchia. In the present paper we turn to the genus *Spinula*, which is represented by five species in our samples. These form a component part of a larger group of species exhibiting a spectrum of characters which we (as others before us) have found difficult to split into well-defined sub-units. All species of the group are characterized by having the shells rostrate posteriorly and at least a portion of the ligament internal. We place these together in a single family, the Nuculanidae, which we divide into three subfamilies: Spinulinae, Ledellinae, and Nuculaninae. The two latter subfamilies will be subjects of later papers in this series.

The proposed division is at variance with the conclusion of Filatova (1958) that *Spinula* is not related to the genus *Leda* (=*Nuculana*) as had been originally maintained by Dall (1908). Filatova (1958, 1976) referred *Spinula* to the family Malletiidae, stating that *Spinula*, in common with other members of this family, has an external ligament. She also noted anterior and posterior rows of fine hinge teeth separated by a toothless area below the umbo and an internal ligament.

Knudsen (1970) believed, as did Yonge (1939), that there is no justification for separating the Malletiidae from the Nuculanidae. For the present, we can state unequivocally that our own extensive material shows that Knudsen (1970) was correct in placing *Spinula* close to *Ledella* and *Nuculana* and that, while *Spinula* and *Ledella* are closely related (Table 1), *Spinula* and *Malletia* are clearly not.

[1] University Marine Biological Station, Millport, Isle of Cumbrae, Scotland KA28 0EG.

[2] Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.

Family NUCULANIDAE Adams and Adams, 1858

Shell laterally compressed, oval in outline except for non-gaping rostrate posterior margin, shell frequently ornamented with concentric lines or ridges; ligament either entirely internal or with internal and external part; posterior siphons present, the inhalent and exhalent lumina of which may or may not be separated by fused tissue.

The three subfamilies may be separated on the form and position of the rostrum.

Subfamily Nuculaninae: rostrum formed as a continuous extension of dorsal shell margin; ventral margin of rostrum forms part of the convex ventral margin of the shell.

Subfamily Ledellinae: rostrum formed as a submedial beaked extension of the posterior shell margin; ventral concave flexure where the base of rostrum meets the convex ventral margin of shell (Table 1).

Subfamily Spinulinae: rostrum formed as a supramedial or occasionally medial extension of the posterior shell margin; ventral concave flexure where base of margin meets convex ventral margin of shell. A detailed diagnosis of this subfamily follows.

Subfamily SPINULINAE

Shell moderately robust, laterally compressed, oval in outline except for non-gaping rostrate posterior margin; rostrum triangulate, supramedial, rarely medial; shell glossy with concentric lines or ridges; ligament amphidetic with small internal triangular resilium and external outer layer extended by fused periostracum; hinge plate with small, chevronshaped teeth; hind gut usually with numerous coils to right side of body or, exceptionally, a single loop to the right; palps moderately large with many narrow palp ridges; adductor muscles unequal in size, the anterior being larger; siphons

formed by fusion of inner muscular mantle lobes ventral to incurrent siphon, no intersiphonal septum present.

Genus *Spinula* Dall, 1908

Type species: *Leda (Spinula) calcar* Dall, 1908, original designation.

The subfamily is monogeneric, *Spinula* being defined identically with the definition of the subfamily.

Two subgenera, *Spinula* and *Bathyspinula* Filatova, 1958 are recognized.

Subgenus *Spinula* Dall, 1908

Type species: as for genus.

Surface of shell with very fine concentric ridges; valves compact, relatively sturdy; periostracum smooth, glossy; tip of rostrum sharp.

Subgenus *Bathyspinula* Filatova, 1958

Type species: *Spinula (Bathyspinula) oceanica* Filatova, 1958, here designated.

In addition to concentric ridges on surface of shell, straight ridges in the form of striae obliquely intersect the concentric ridges; tip of rostrum blunt and rounded.

WORLD LIST OF *SPINULA* (NOT INCLUDING PRESENT RECORDS)

Spinula calcar (Dall, 1908). Recorded from the Pacific (4067–5535 m). See: Dall (1908); Hertlein and Strong (1940); Filatova (1958, 1976); Wolff (1960); Clarke (1962); Belyaev (1966); Knudsen (1970); Okutani (1974, 1975). *Spinula calcarella* (Dall, 1908) is now regarded as being identical to *S. calcar* (Knudsen, 1970; Filatova, 1976), although Filatova (1958) originally regarded it as a subspecies of *S. calcar* and not a *Bathyspinula.* We have not recorded this species in the Atlantic.

Spinula subexcisa (Dautzenberg and Fischer, 1897) (=*S. excisa* of authors, *non S. excisa* Philippi, 1844). Supposedly recorded throughout the following Basins (see p. 21): Labrador, N. America, Norway, W. Europe, Argentine, Agulhas, Angola, and the Mid-Atlantic Ridge in the region of the

Table 1. Comparison of subfamilies Ledellinae and Spinulinae.

Ledellinae	Spinulinae
1) Adductors equal in size or almost so.	1) Adductors unequal, posterior ⅓ size of anterior.
2) Posterior margin rostrate, medial or submedial.	2) Posterior margin rostrate, supramedial (rarely medial).
3) Ligament amphidetic, usually internal (except in *L. kermadecensis*); short central, inner and outer layers between hinge plates extended by fused periostracum.	3) Ligament amphidetic, with well-developed external part; internal part inset as resilium into hinge plate below umbo, externally extended by outer layer and fused periostracum.
4) Hind gut not spirally coiled to right (except in *L. crassa*, which is similar to *Spinula*).	4) Hind gut spirally coiled to right (except in *S. calcar*, which Knudsen [1970] figures with a single loop).
5) Shell robust, moderately inflated, usually with a matt surface; in some species, after reaching a given size, a change in spiral angle of growth produces a flattened shell margin.	5) Shell moderately robust, usually compressed, with glossy surface; no change in spiral angle of growth of shell.
6) Palps with (<30) palp ridges that are not exceptionally narrow.	6) Palps with numerous (<50) narrow palp ridges. Species of an equivalent size with 1½ to 2 times as many ridges as in *Ledella*.

Azores (1848–5153 m). See: Jeffreys (1876, 1879); Smith (1885); Clarke (1962).

Spinula pelvisshikokuensis Okutani, 1975. Recorded from the northwestern Pacific (3610 m). See: Okutani (1975).

Spinula filatovae Knudsen, 1967. Recorded from Gulf of Aden (2312 m). See: Knudsen (1967); Filatova (1976).

Spinula kermadecensis Knudsen, 1970. Recorded from Kermadec Trench (5850–5900 m). See: Knudsen (1970).

Spinula tasmanica Knudsen, 1970. Recorded from Tasman Sea (3580 m). See: Knudsen (1970); Filatova (1976).

Spinula sp. (Knudsen, 1970). Recorded from the Bay of Bengal (2820 m). See: Knudsen (1970).

Spinula (Bathyspinula) bogorovi Filatova, 1958. Recorded from the Riu Kiu Trench (6726 m). See: Filatova (1958); Wolff (1960); Clarke (1962); Belyaev (1966); Knudsen (1970); Filatova (1976).

Spinula (Bathyspinula) oceanica Filatova, 1958. Recorded from Japan Trench and northwestern Pacific (4653–6293 m). See: Filatova (1958, 1976); Wolff (1960); Suyehiro *et al.* (1962); Clarke (1962); Knudsen (1970); Okutani (1974).

Spinula (Bathyspinula) vityazi Filatova, 1964. Recorded from the Kurile-Kamchatka Trench (6435–9335 m). See: Filatova (1964, 1976); Wolff (1960) [*S. (B.) vitiazi—n. nudum*]; Suyehiro *et al.* (1962) (*S. sp.*); Clarke (1962) [*S. (B.) vityazi—n. nudum*]; Belyaev (1966); Knudsen (1970); Okutani (1974).

Spinula (Bathyspinula) knudseni Filatova, 1976.

Recorded from the Kurile-Kamchatka Trench (6400–6800 m). See: Filatova (1976).

Spinula (Bathyspinula) thorsoni Filatova, 1976. Recorded from the Romanche Trench (6380–6430 m) and the Puerto Rico Trench (5220–6400 m). See: Filatova (1976).

SPECIES OF *SPINULA* FROM THE ATLANTIC

Spinula filatovae Knudsen, 1967
Figures 1–7 + 28

Spinula filatovae Knudsen, 1967: 257, fig. 8; Filatova, 1976: 219. (Type locality: JOHN MURRAY Expedition, Station 26, Gulf of Aden, Lat. 12°29′30″N, Long. 50°51′30″E; Holotype: BM(NH) 196640W.)

Previous records: Gulf of Aden, 2312 m (Knudsen, 1967). Western Indian Ocean, 3152–4340 m (Filatova, 1976).

Present records: Depth range = 1261–4340 m.

Specific Description. Knudsen (1967) described this species from one specimen taken from the Gulf of Aden; the soft parts were not studied in detail. The present specimens, all from the eastern Atlantic, are in sufficient number to confirm and extend Knudsen's description.
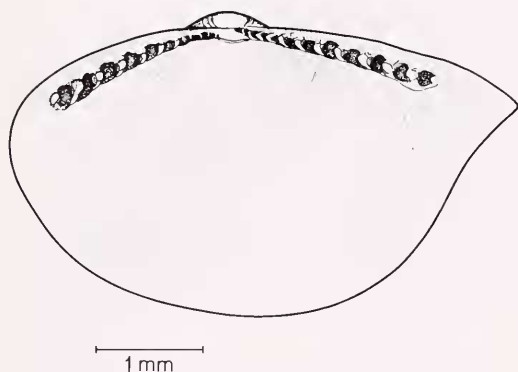
Figure 1. *Spinula filatovae*. Internal view of right valve of a specimen from Station S44 to show details of the hinge plate and shell outline.

Shell thin, with moderately strong concentric ridges, elongate-oval in outline with pointed posterior rostral extension; umbos somewhat anterior, low, beaks curved medially; dorsal margin weakly convex; antero-dorsal margin proximally straight and sloping downward to form smooth curve with anterior margin; postero-dorsal margin slightly convex, smoothly curved; rostrum short, sharply pointed, separated from ventral margin by slight sinuosity; ventral margin long, moderately convex, smoothly curved; an- terior margin short, smoothly rounded; a ridge or keel, better developed distally, extends from umbo to point of rostral ex- tension; postero-dorsally concentric ribs form right angles, the point of origin of which coincides with ridge; hinge plate long, rather narrow, anterior and poste- rior hinge plates with 10–12 chevron- shaped teeth, distal 5 in each series strong, proximal teeth progressively smaller, the innermost very reduced and difficult to discern; ligament amphidetic, internal part (resilium) small, approxi- mately as long as wide, triangulate with truncated apex, outer layer externally ex- tended anteriorly and posteriorly by fused periostracum to the level of the in- sertion of the sixth* tooth of both anterior and posterior hinge-tooth series (Fig. 1). Larval shell 385 μm in length; maximum recorded shell length 6.1 mm.

Our specimens correspond in most re- spects with *Spinula filatovae* as de- scribed by Knudsen (1967), but we would not regard the shell as thick when com- pared with species of the related genus *Ledella*. However, this is a subjective term, and there is no doubt that for an

---

* Numbered from the distal ends of the series.

TABLE 2.   RECORDS FOR *Spinula filatovae* KNUDSEN.

Cruise	No.	Station no.	Depth (m)	No. of specimens	Latitude	Longitude	Gear	Date
				West Europe Basin				
SARSIA	—	S.44	1739	43	43°40.8′N	3°35.2′W	ES*	16.7.69
SARSIA	—	7610	1100–1185	12	43°42.5′N	3°48.6′W	Agassiz Dredge	10.9.76
				Cape Verde Basin				
ATLANTIS II	31	142	1624–1796	19	10°30.0′N	17°51.5′W	ES	5.2.67
				Guinea Basin				
WALDA	—	DS27	1261	1	3°30.7′N	5°31.8′E	ES	30.8.71
WALDA	—	DS28	1376	49	4°21.2′N	4°35.2′E	ES	30.8.71

* Epibenthic sled.

abyssal species this has a well-calcified shell. The figure of the type (Knudsen, 1967), admirably drawn by the late Paul Winther, is entirely accurate. Only S. *tasmanica* approaches the present species in general shape (Knudsen, 1970), but it differs in being stouter, having a heavy hinge plate with massive teeth, and having a more prominent posterior rostrum.

The amphidetic ligament consists of a small, triangular wedge-shaped internal part, the resilium, and an external part extending anterior and posterior to the umbo. The dorsal surface of the resilium is visible externally and consists of an inner layer overlain dorsally and distally and to some extent laterally by the outer layer. Dorsally, the resilium is overlain by a thin layer of fused periostracum. The external ligament is arched, elongate, and spindle-shaped in outline. It is connected anteriorly and posteriorly to the internal ligament by a very narrow neck of material. The external extensions of the ligament comprise an outer layer and thickened fused periostracum, the latter extending beyond the limits of the outer layer.

Morphology. With the exception of the posterior margin, the structure of the mantle is little modified. The mantle edge is for the most part not fused. Posteriorly, a combined inhalent and exhalent siphon is present, formed by fusion of inner muscular mantle lobe. A specialized area below the siphon almost certainly marks the point at which the palp proboscides are extended onto the sediment. A single siphonal tentacle is present on the left or right side, and on the anteroventral mantle margin there is a pair of anterior sense organs. Both of these structures are specializations of the middle sensory mantle lobe (see p. 24).

The siphons, combined as a somewhat laterally compressed tube, possess internally and laterally a series of ridges, of which one pair (left and right midlateral) originates from the posterior ends of the gill axes. Within the ridges, between inner and outer epithelium, a regular series of fine longitudinal muscle strands lie parallel to and equally spaced from each other (Figs. 2, 19). There is little or no hemocoelic space within the siphon. It is doubtful if the low-crested lateral ridges permanently separate an inhalent from an exhalent part by their approximation. No interlocking cilia can be seen in section. Scattered mucous cells are present in the inner epithelium. The anus lies immediately dorsal to the inner limit of the siphon, above the origin of the axial ridges, so that faeces tend to be extruded into the dorsal half of the siphonal tube. The ridges almost certainly act as guides for the passage of the faeces. The diameter of the faecal rod is about half the height of the lumen of the siphon, and fragments of the faecal rod have been observed dorsally. The gills act as a pump; thus on the upstroke faeces may be extruded as water is passing anteriorly along the lower half of the lumen due to the reduced pressure within the lower part of the mantle cavity. As in all protobranchs, the faecal rod is solid and does not easily fragment. Alternatively, water could pass into the mantle via the feeding aperture ventral to the siphons, although this is unlikely if the animal is buried to the extent its morphology suggests (see p. 28). The siphons can be completely retracted within the shell and are extended from a position immediately ventral to the posterior rostral extension of the shell. In the retracted state, the siphons are bent into an S-shape. Three retractor muscles extend into the mantle tissue at the posterior limit of the siphonal embayment.

Ventral to the siphons is a broad and deep specialized area of the mantle that is undoubtedly associated with feeding and which we refer to as the feeding aperture (Sanders and Allen, 1977) (Fig. 2). Here, the inner mantle lobe is enlarged both in thickness and width and much folded in the contracted state. Immediately *internal* to the muscular lobe is an
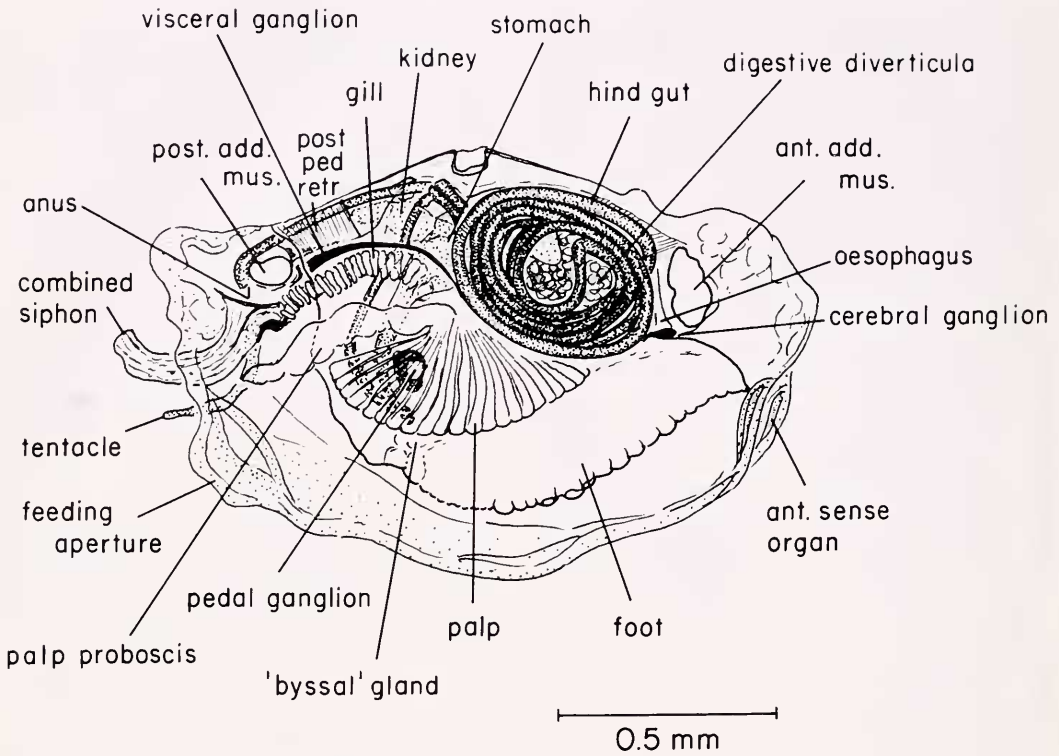
Figure 2.   *Spinula filatovae.* Semidiagrammatic view of right side of the animal to show disposition of the organs.

additional lobe that is thinner and nar-
rower than the former, but which lies par-
allel to it and extends the length of the
feeding aperture. The epithelium on the
ventral side of the additional lobe, the
dorsal side of the muscular lobe, and the
epithelium between the two, is richly
supplied with acidophilic gland cells.
This band of gland cells is continued an-
teriorly to the inside of the inner mus-
cular lobe, although the cells here are
fewer in number. Internal to the feeding
aperture, there is a series of fine radiating
pallial retractor muscles, and it is clear
that this area of the mantle is capable of
considerable extension. The tips of the
contracted palp proboscides lie close to
the second mantle lobe. Although there
is no fusion ventrally to form a separate
aperture, the opposing inner muscular

lobes undoubtedly come together at this
point and thus separate the feeding ap-
erture from the extensive pedal gape.

The adductor muscles are unequal in
size (Fig. 2), with the 'quick' and 'catch'
parts obvious (Fig. 4). The smaller pos-
terior adductor muscle is pear-shaped in
outline. The anterior adductor is cres-
cent-shaped and about 2.5 times as large
in cross section as the posterior. Imme-
diately below the anterior adductor, at
the mantle edge, is the anterior sense or-
gan (see p. 24). A single siphonal tenta-
cle, common to many protobranch bi-
valves, arises from a short pocket on
either the right or left side of the base of
the siphon. The tentacle is developed
from the middle sensory lobe of the man-
tle. It consists of an elongate, finely ta-
pering cone which in transverse section

comprises a single outer layer of large cuboid epithelial cells which appear finely granular and may be secretory (Fig. 26a). To the inside is a single layer of elongate connective-tissue cells between which are scattered gland cells with ducts to the outside. In the central core is a large nerve together with a few fine muscle cells. As in the case of the siphon, although there is some hemocoelic space, it is not large. The tentacle clearly has a sensory function, but it may also assist in the cleansing of the siphonal region, including the feeding aperture.

The gills lie parallel to the dorsal posterior shell margin (Fig. 2). They are well developed with approximately 26 gill plates to each side of the axis. The outer and inner demibranchs are attached to the mantle and body, respectively, by tissue juctions. Posterior to the foot, the last three or four plates of the opposing inner demibranchs join. The gill axes join with the siphonal ridges.

The palps are moderately large and, depending on the size of the animal, have approximately 25–50 closely spaced ridges on their inner faces. The palp proboscides are relatively slender. The palps extend across the posterior quarter of the body. The mouth is set behind, but close to, the anterior adductor muscle.

The foot is extremely well developed and of typical nuculanid form, having a narrow base (Fig. 3). The divided sole is elongate and has finely papillate edges. Due to the presence internally of a large 'byssal' gland, the posterior ventral margin of the foot bulges laterally. A highly muscular foot must indicate active locomotion.

The posterior pedal retractor muscles comprise a thick, wide strap that inserts onto the shell on either side of the hind gut anterior to the posterior adductor muscle (Fig. 2). There is also a small postero-lateral muscle lying immediately posterior to the stomach (Fig. 4). Three major pairs of anterior pedal retractor muscles arise anteriorly from the base of
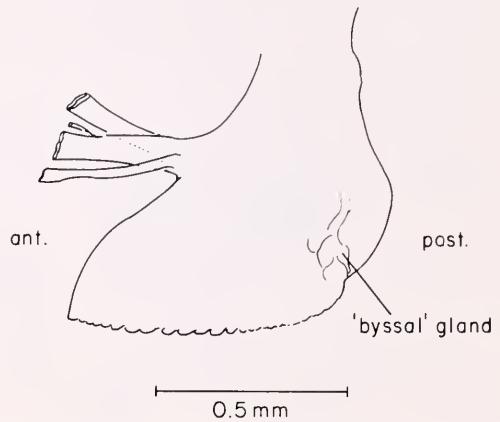

Figure 3. *Spinula filatovae.* Lateral view of the foot to show position of the left series of anterior pedal retractor muscles.

the foot and insert posterior to the anterior adductor on either side of the oesophagus (Fig. 4a). These overlap one another where they join the foot: the innermost muscle having the most posterior insertion on the shell; the outermost, the most anterior insertion. In section, the innermost muscle is seen to be split in the sagittal plane.

The cerebral ganglia are relatively small while the visceral are elongate. The pedal ganglia, which are the largest, lie far posterior within the foot close to the mid gut and are relatively ventral in position in comparison with other protobranch bivalves (Fig. 2). A large statocyst is associated with each pedal ganglion and lies dorsal to it.

The mouth is displaced posteriorly to a small extent; it opens to a relatively long oesophagus that curves anteriorly to the posterior face of the anterior adductor before passing posteriorly to the stomach. The oesophagus widens considerably just before joining the stomach (Fig. 4a). The stomach and style sac lie diagonally within the body.

The stomach and style sac are huge, taking up most of the central body space. The stomach externally is dark brown in
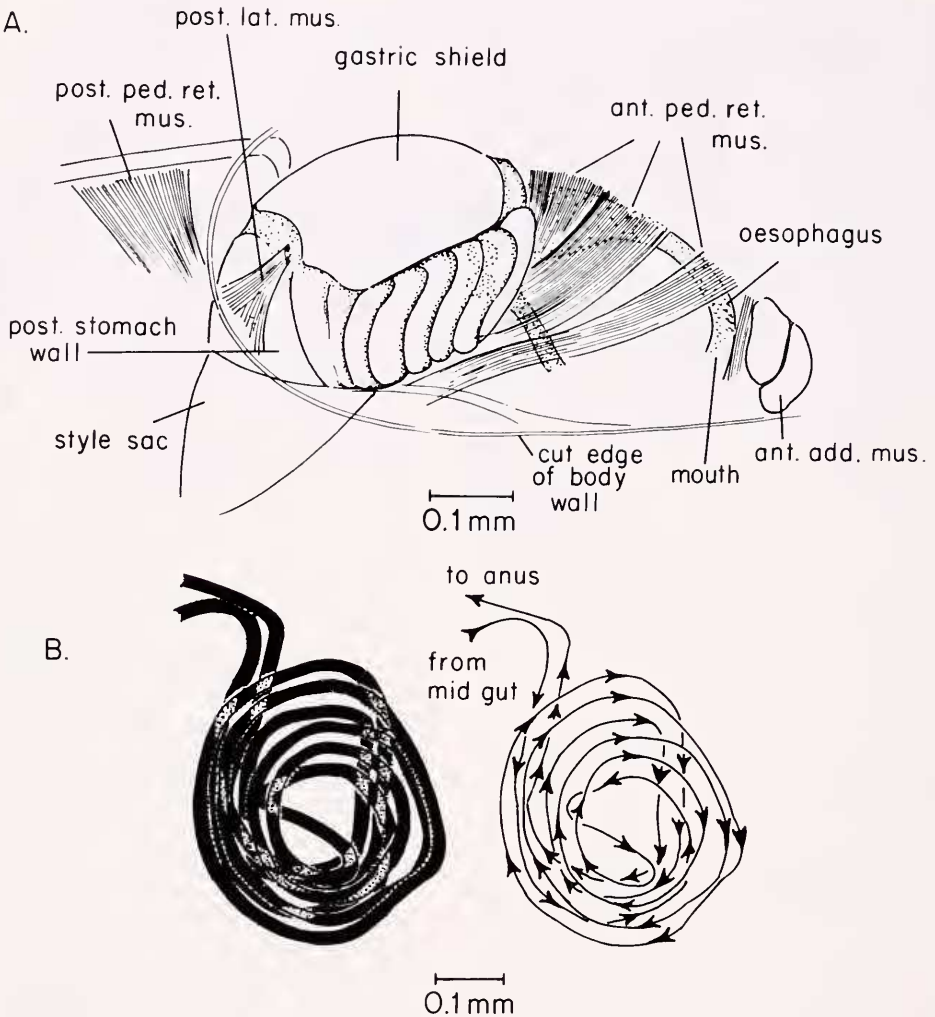
Figure 4. *Spinula filatovae.* A. Detail of the external features of the right side of the stomach and associated pedal muscles. B. Detail of the disposition of the hind gut coils viewed from the right side.

color. There is a large gastric shield that occupies more than one-third of the stomach wall. It is antero-dorsal in position and extends laterally, but more extensively to the left than to the right (Fig. 5). The remaining anterior wall is occupied by eight broad ciliated ridges (Fig. 4a), and at their anterior limit there are the apertures of three ducts leading to the digestive diverticula. The posterior wall

of the stomach adjacent to the style sac appears to be without ridges. The stomach is cradled by the anterior, posterior, and postero-lateral pedal retractor muscles which must, on contraction, exert a considerable pressure on the stomach and constitute a major force pushing material through the gut. It is probably significant that the digestive ducts are far anterior and thus are anterior to the main

muscular force. As a result, material will not be squeezed into the digestive gland. Although the hind gut is ciliated and without obvious musculature, it is doubtful whether the cilia can be the main motive force moving material in the long hind gut. There is little or no space between faecal rod and gut wall.

From a position dorsal to the pedal ganglia, the hind gut passes posterior to the ganglia deep into the foot and curves antero-ventrally to the ganglia. It then retraces a course parallel to the descending section before passing to the right side of the body at a point immediately below the internal ligament. On the right side, the hind gut forms six tightly packed coils (Fig. 4b) before passing mid-dorsally over the posterior adductor muscle to the anus. There is no penetration by the body tissue of the blood space of the right mantle such as is seen in the Tindariidae (Sanders and Allen, 1977). There is no typhlosole present in the hind gut.

Material in the gut consists of fine clay particles and various skeletal remains that are too finely fragmented to identify except to note that many are pieces of diatom frustules belonging to many species. Material in the stomach looks little different from that in the hind gut. Little or no material is present in the lumen of the digestive tubules, and no skeletal remains were noted in the tubule cells.

The digestive gland is present both to the right and left of the body and, for the most part, lies anterior to the stomach. On the right side it is surrounded by the coils of the gut (Figs. 2, 5). There are three primary ducts leading from the digestive gland, two on the left side of the stomach below the base of the exceptionally large tooth on the gastric shield and a third, slightly more anterior, on the right ventral wall of the stomach (Fig. 5).

The digestive gland cells are similar to those seen in other protobranch bivalves. Interstitial cells are scattered at the periphery of the tubules, and some of these,
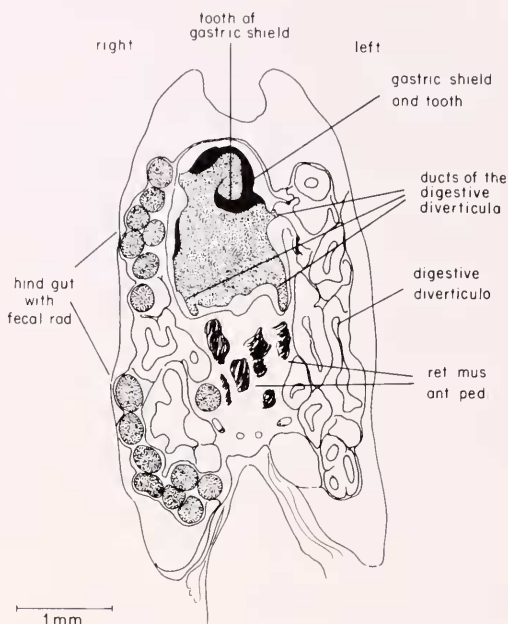

Figure 5. *Spinula filatovae.* Transverse section through viscera to show stomach and hind gut coils.

like the epithelial cells of the digestive ducts, contain highly refractile golden granules in the cytoplasm. In section, the vacuolated cells appear to be actively cutting off spherules into the lumen of the tubule. In addition, at the base of many of the vacuolated cells, there are clear spherical inclusions which may be the contents of vacuoles. From the apparent lack of food material in the tubule cells, it seems almost certain that much, if not all, digestion is extracellular. The kidney is moderately large and, as a feature common to many deep-sea bivalves (Allen and Turner, 1974; Oliver and Allen, personal observation), extends forward on either side of the posterior half of the stomach. A single layer of cuboid epithelial cells lines the wall of the kidney. The lumina of the left and right sides cross-connect below the hind gut posterior to the point where the hind gut passes through the ventricle of the heart.

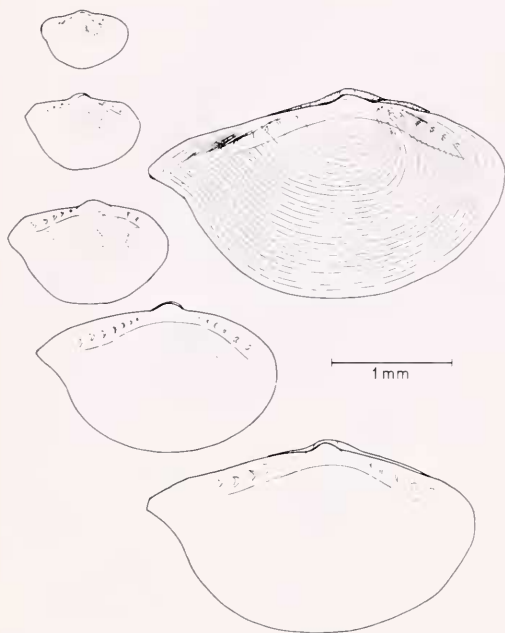*Reproduction.* Sexes are separate; go-

Figure 6. *Spinula filatovae.* Lateral views of a series of specimens to show change in shell outline with increasing size.

nads were only observed in a few specimens of 2.6 mm total length and above. Egg numbers are small, about 20 in a specimen of 2.6 mm. Several of the larger specimens (3.9 mm) appear to be spent. The gonads overlie the lateral and dorsal side of the viscera and are in a similar position on each side of the body. Because of lack of maturity, maximum egg diameter could not be determined. At maximum the gonad forms a ring around the coils of the hind gut or, on the left, the digestive diverticula. For the most part, the larger the animal the more mature is the gonad; however, not all large specimens have maturing gonads. The gonadal aperture lies close to the apertures of the kidney, anterior to the posterior pedal retractor muscles.

Growth. The larval shell is large (approx. 385 μm in length). The adult shell and rostrum become relatively more elongate with growth. Height to total length ratios and posterior length (=distance from umbo to distal margin) to total length ratios confirm the visual observation (Figs. 6, 7). The minimum length recorded is 1.2 mm, the maximum 6.1 mm. Both of the largest samples (D.S. 28 and S. 44) from the Canaries and Biscay respectively have similar length frequency histogram to size range (Fig. 7). There are no clear peaks to be seen, suggesting perhaps that the production is not confined to a short breeding season.

Spinula sp.
Figures 8–10 + 28

Records: Depth range = 4800–5000 m.

Because two of the three specimens have been lost and the third has been decalcified and made into a slide for the study of its soft-part anatomy, this species will not be named.

Description. Shell stout, thick, with strong, even, concentric ridges, somewhat elongate-oval in outline, rostrum short, bluntly pointed; umbos raised, moderately prominent, inflated, slightly posterior of middle, beaks medially curved; dorsal margin strongly convex; longer antero-dorsal margin slopes sharply downward to form smooth curve with anterior margin; shorter postero-dorsal margin almost straight to about level of distal end of posterior hinge plate, thereafter angled ventrally to form short, blunt rostrum separated from ventral margin by slight sinuosity; ventral margin long, moderately convex, smoothly curved; weak, although wide, keel extends from umbonal region to limit of rostrum; concentric ridges turn sharply at right angles where they cross the keel; hinge plate broad, strong, relatively long; anterior and posterior hinge plates with about 10 chevron-shaped teeth, distal 5 large and strong, more proximal teeth progressively smaller, most medial teeth so reduced as to be difficult to see; ligament amphidetic, internal part (resilium) large and
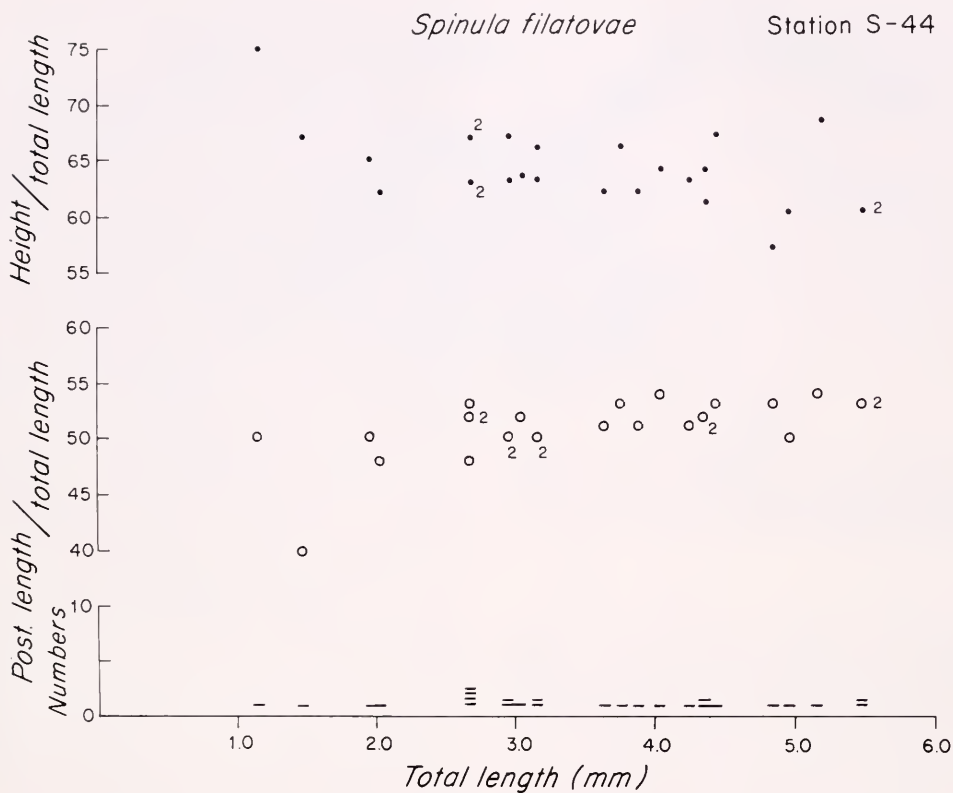
Figure 7. *Spinula filatovae.* Changing shell shape with increasing size as measured by the ratios height/total length and posterior shell length (umbo-rostrum)/total length to total length.

triangulate, with external extension elongate, narrow, anterior and posterior parts of approximately equal length, extending to level of fifth tooth, both on anterior and posterior hinge plate. Maximum recorded shell length 3.8 mm.

Of other described species of *Spinula*, only *S. tasmanica* has such a thick hinge plate and large teeth (Fig. 8); however, *S. tasmanica* is more elongate with a sharply pointed rostrum and with a low umbo clearly anterior in position (Knudsen, 1970).

Morphology. As we have only three specimens of this species, sections were not taken, and the following description is from a single specimen as a whole mount stained in hematoxylin (MCZ 279903).

The mantle structures differ little from those described for *Spinula filatovae.* The combined siphon is particularly large and deep. The feeding aperture is extensive, and the inner mantle lobe is extremely deep. It should be noted that the ventral posterior corner of the foot is extended and lies close to the feeding aperture and may well aid in pushing out the pseudofaeces from the mantle cavity, as happens in other protobranch bivalves.

The anterior sense organ is far anterior, in advance of the anterior limit of the anterior adductor muscle.

The adductor muscles are markedly unequal in size. The posterior muscle is oval, the long axis parallel to the dorsal margin of the shell. The anterior adduc-
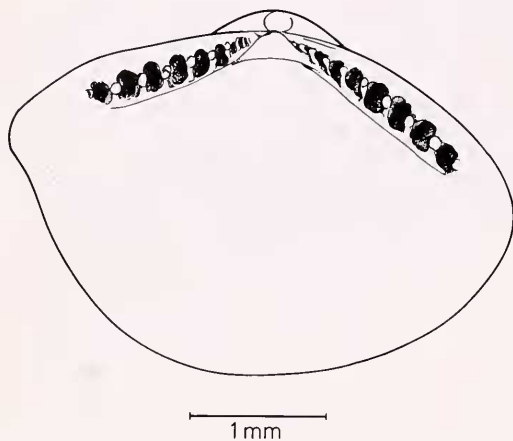
Figure 8. Unnamed species of *Spinula*. Internal view of left valve of a specimen from Station 83 to show details of hinge plates and shell outline.

tor muscle is more rounded, the larger 'quick' and smaller 'catch' parts being clearly visible. The siphonal tentacle originates on the right side and is inserted close to the base of the siphon.

The foot, while large, is not as large as it is in the other species described here. However, the 'byssal' gland is extremely large and spherical in form.

The gills are carried high in the mantle cavity parallel to the postero-dorsal shell margin. Thirteen gill plates are present on each demibranch in the present specimen. The mouth is set just posterior to the anterior adductor, the palps extending little more than half way across the body. In this specimen there are 30 fine ridges; the anterior part of the right palps is overlain by the coils of the hind gut.

The contracted palp proboscides are noticeably short and stubby.

The stomach and style sac are relatively small, barely extending into the ventral half of the foot. Similarly, the hind gut does not extend deep into the foot, as is the case in *Spinula filatova*. Like the latter species, the first section of the hind gut lies close to the posterior body wall and extends just ventral to the pedal ganglion, where it turns dorsally taking one V-turn behind the stomach before passing to the right side of the body at a point close to the posterior dorsal margin of the shell. It forms seven visible coils on the right hand side of the body which are stacked one above the other; each coil is offset in an anterior direction adjacent to the anterior inner hinge margin.

The pedal ganglion is large, positioned in the posterior part of the neck of the foot. The visceral ganglion is cylindrical, terminating close to the posterior adductor muscle. The visceral-cerebral commissure parallels the gill axis and the ventral margin of the coils of the hind gut. Unfortunately, the specimen is a maturing male, so the cerebral ganglion and part of the hind gut are obscured by the testis.

Spinula hilleri new species
Figures 11–15 + 28

Specific Description. Shell moderately strong and slender, ornamented with

TABLE 3.   RECORDS FOR *Spinula* sp.

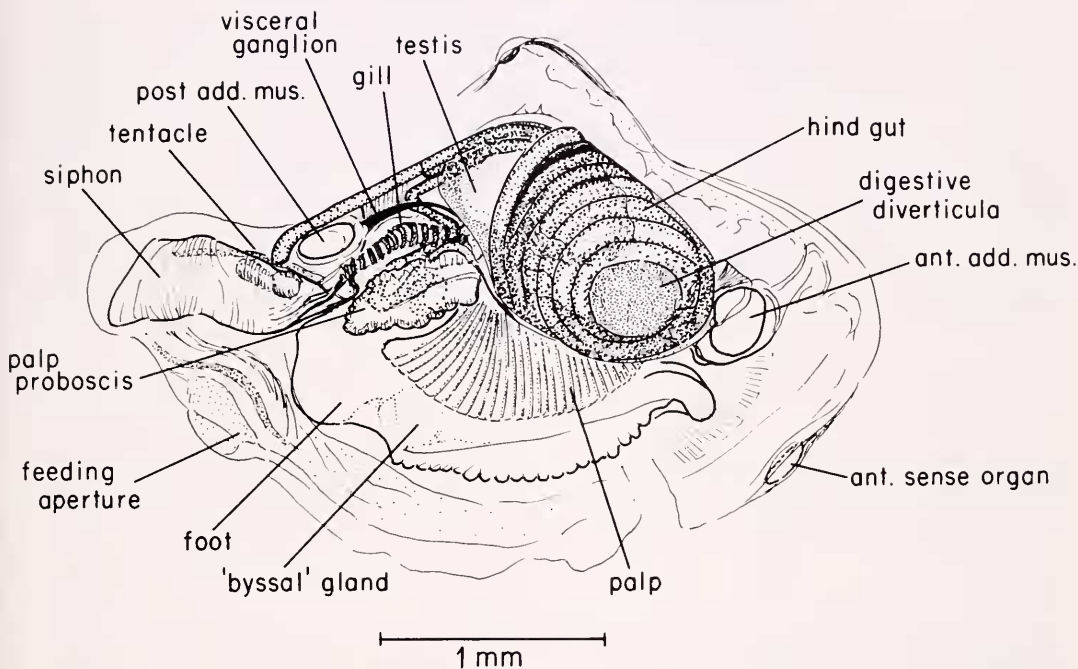| Cruise	No.	Station no.	Depth (m)	No. of specimens	Latitude	Longitude	Gear	Date
North America Basin								
ATLANTIS II	24	121	4800	1	35°50.0′N	65°11.0′W	ES	21.8.66
ATLANTIS II	24	123	4853	1	37°29.0′N	64°14.0′W	ES	22.8.66
CHAIN	50	83	5000	1	34°46.5′N	66°30.0′W	ES	3.7.65

Figure 9. Unnamed species of *Spinula*. Semidiagrammatic view of right side of the animal to show disposition of the organs.

even concentric ridges; rostrum short, sharply pointed; umbos slightly anterior in position, in larger specimens small with low profile, beaks medially curve; dorsal margin moderately convex; antero-dorsal margin sloping sharply to form smooth curve with anterior margin; pos-tero-dorsal margin nearly straight be-tween umbo and distal edge of hinge plate, thereafter angling abruptly to form a short, usually sharp, pointed rostrum demarked from ventral margin by a con-cave sinuosity; ventral margin long, smoothly curved, convex, with greatest convexity in larger shells adjacent to pos-terior sinus (i.e., maximum shell height posterior to umbo); keel present, extend-ing from umbo to point of rostrum, weak-ly developed near rostrum, becoming strong anteriorly where concentric lines form a sharp angle; hinge broad, strong and relatively long; anterior hinge plate
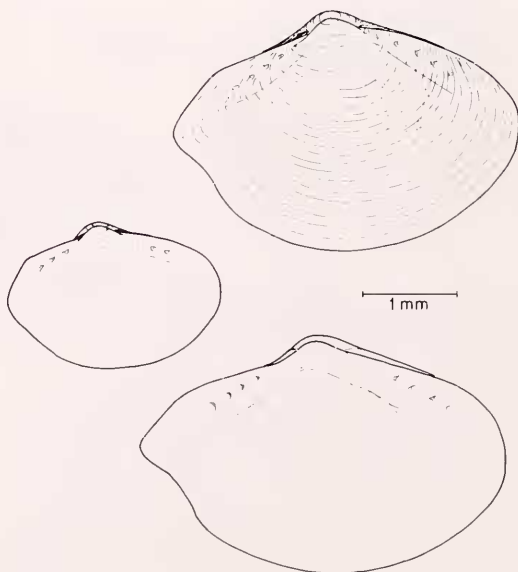

Figure 10. Unnamed species of *Spinula*. Lateral views of the three specimens recorded from our samples, to show variation in the shell outline.

TABLE 4.   RECORDS FOR *Spinula hilleri* NEW SPECIES.

Cruise	No.	Station no.	Depth (m)	No. of speci- mens	Latitude	Longitude	Gear	Date
				Angola Basin				
ATLANTIS II	42	195	3797	98	14°49.0′– 14°40.0′S	9°56.0′– 9°54.0′E	ES	19.5.68
ATLANTIS II	42	196	4612–4630	2	10°29.0′S	9°03.0′– 9°04.0′E	ES	21.5.68
ATLANTIS II	42	197	4592–4597	9	10°29.0′S	9°40.0′E	ES	21.5.68
ATLANTIS II	42	198	4559–4566	3	10°24.0′S	9°09.0′E	ES	21.5.68
WALDA		CY13	2044	3	12°03.7′S	12°22.3′E	T*	10.7.71
				Cape Verde Basin				
ATLANTIS II	31	145	2842–2891	1	10°39.5′N	17°44.5′W	ES	6.2.67
				Canary Basin				
DISCOVERY		6710	2670	1	27°23.6′N	15°39.6′W	ES	19.3.68
DISCOVERY		6711	2988	1	27°14.9′N	15°36.3′W	ES	19.3.68
				Sierra Leone Basin				
WALDA		CY21	3034	1	0°40.1′S	6°48.8′E	T	1.8.71
WALDA		CY23	2231	2	0°45.1′N	8°27.2′E	T	2.8.71
				West Europe Basin				
CHAIN	106	323	3350	1	50°08.3′N	13°53.7′W	ES	21.8.72
POLYGAS		DS15	2264	1	47°35.2′N	8°46.1′W	ES	23.10.72
				Brazil Basin				
ATLANTIS II	31	155	3730–3783	4	0°03.0′S	27°48.0′W	ES	13.2.67
ATLANTIS II	31	156	3459	8	0°46.0′– 0°46.5′S	29°28.0′– 29°24.0′W	ES	14.2.67
				Argentine Basin				
ATLANTIS II	60	242	4382–4405	5	38°16.9′S	51°56.1′W	ES	13.3.71
ATLANTIS II	60	247	5209–5227	24	43°33.0′S	48°58.0′W	ES	17.3.71
				Guiana Basin				
KNORR	25	303	2842–2853	4	8°28.8′N	56°04.5′W	ES	1.3.72
KNORR	25	306	3392–3429	5	9°31.1′N	56°20.6′W	ES	2.3.72

* Trawl.

with about 13 chevron-shaped teeth, posterior hinge plate with about 11 teeth (number depending on size of animal); distal teeth strong and well developed, proximal teeth progressively smaller, with those bordering the internal ligament minute and rudimentary; ligament amphidetic, internal part (resilium) triangulate, external extensions elongate, equal in length, and extending to level of fifth or sixth tooth. Maximum recorded shell length 8.7 mm.

We name this species after Captain Emerson Hiller of the Woods Hole Oceanographic Institution, whose superb seamanship has enabled us to trawl successfully at greath depths and with great precision throughout the Atlantic Ocean.

Morphology. Spinula hilleri has essentially the same morphology as the other species described here (Fig. 12). Mantle structures differ only in that the combined siphon appears to be very large, even in the contracted state, and that the anterior sense organ lies far anterior. The adductor muscles are relatively small and

unequal in size, the anterior being 2 to 3 times the size of the posterior.

The gills are moderately small, each with approximately 21 plates to each demibranch. The palps are large, with as many as 33 fine ridges; the number, as in the case of the gill plates, is dependent on the size of the individual.

The foot, although slender, is very large in this species, with a more anteriorly directed attitude than in *S. filatovae* and the unnamed species. There is a considerable number of fringing papillae which are somewhat larger than in the other species. The form of the foot suggests that this is an active, fast moving species. In fact, it is probably no coincidence that in this species the adductor muscles are relatively small, there possibly being no prolonged closure of the shell. In contrast, the pedal retractor muscles are well developed and may well assist in the adduction of the valves when the foot is fully contracted (Allen
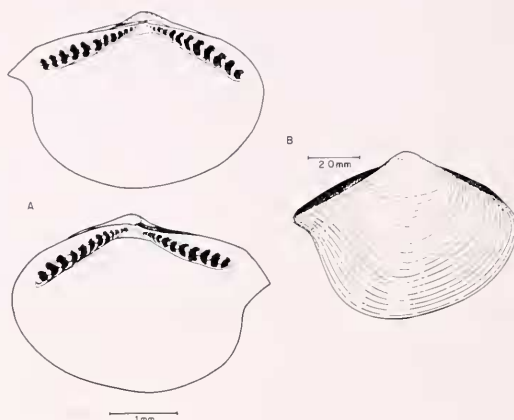
Figure 11. *Spinula hilleri.* A. Internal views of right and left valves of a specimen from Station 155 to show details of hinge plates and shell outline. B. Lateral view of right valve of holotype (MCZ 279904) from Station 195.

and Sanders, 1969). Probably also associated with increased activity is the large size of the ganglia, in particular the pedal. The heel of the foot is extended pos-
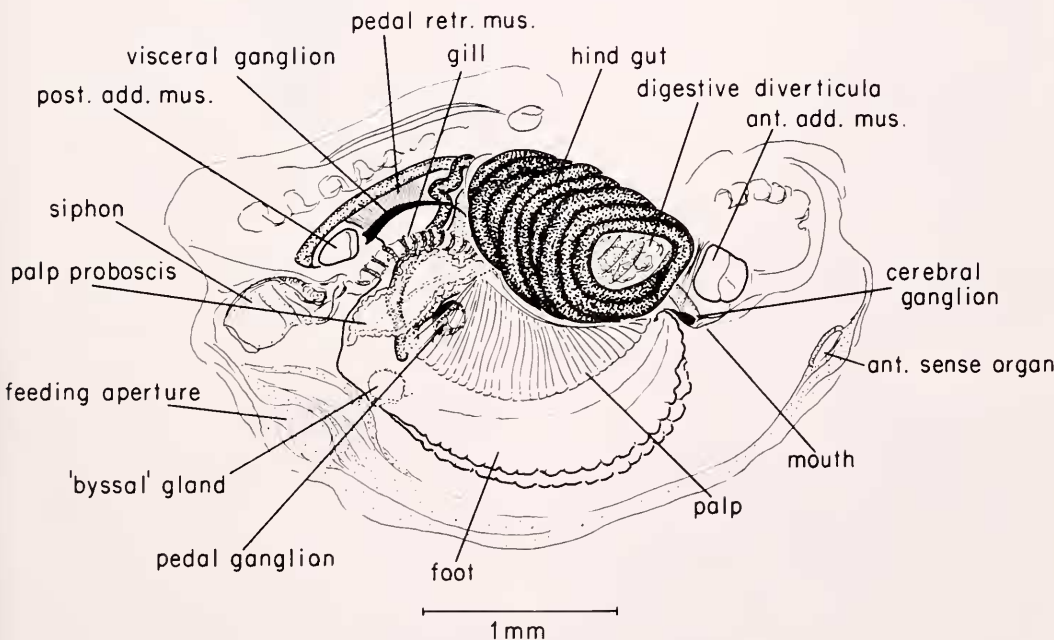
Figure 12. *Spinula hilleri.* Semidiagrammatic view of right side of the animal to show disposition of the organs.
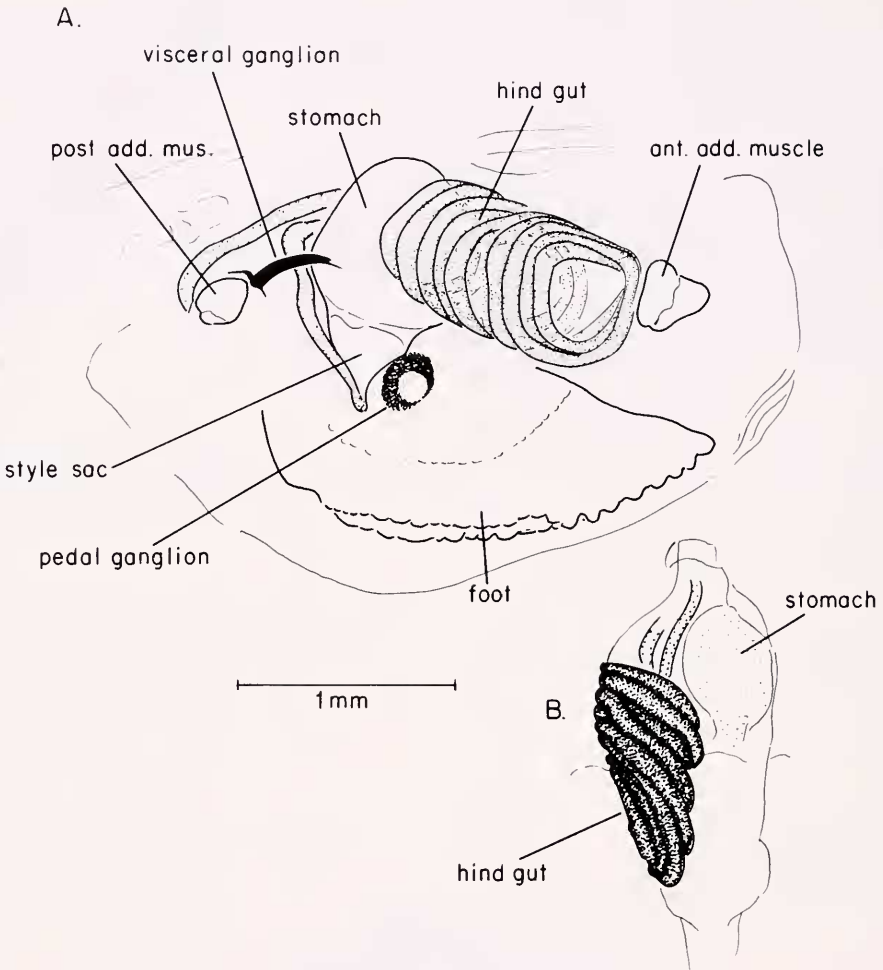
Figure 13.   *Spinula hilleri.* A. Semidiagrammatic view of right side of animal showing an additional hind gut coil, as well as the position of the stomach with respect to the hind gut. B. Hind gut coils as seen from the dorsal side.

teriorly, and there is a well-developed 'byssal' gland.

Usually there are 9 coils to the hind gut, although we have seen a few whole mounts with 8 or 10 coils. From dissection, we believe that in those which appear to have 8 coils there is a hidden coil, while the single case of 10 coils is an exception to the general rule. The coils, although close together in *S. hilleri*, spread in an overlapping sequence from a point just anterior to the umbo anteriorly to the anterior adductor muscle, the outermost coil abutting the posterior edge of the muscle (Fig. 13). Probably because the hind gut takes up so much anterior space, the stomach and style sac are far posterior within the body and far over on the left side. The stomach in protobranch bivalves is normally situated on the left, but usually not so far to the left as in *S. hilleri*. The first section of the hind gut

lies posterior to the pedal ganglion but barely penetrates the foot below the level of the pedal ganglion (Fig. 13).

Because there are so few large specimens, none were opened to observe the condition of the gonads. However, the smallest specimen to show signs of gonadal development was a male, 2.4 mm in total length. In this specimen, the testis was in a very early stage of development and tenuously covered both the posterior part of the coiled hind gut on the right and the digestive diverticula on the left. There was little development of gonadal tissue in other specimens.

Growth stages from the Angola Basin (Station 195) and the Brazil Basin (Station 156) were examined. The larger specimens from the eastern Atlantic tend to have a sharper rostrum than similar sized specimens from the west (Fig. 14). Slight interpopulation differences in lateral outline did not exceed variation exhibited in a single sample. In the course of growth, the rostrum becomes more pronounced (note a gradual change in the total length/umbo-rostral length ratio, Fig. 15). The postero-ventral margin is more angular in young stages than in older shells, but there is little or no change in the height/length ratio. We have no doubt that the populations of the various basins belong to one and the same species. The larval shell measures 420 μm.

Figure 14. *Spinula hilleri*. Lateral views of a series of specimens to show variations in shell outline, with age and geographical locality.

Spinula scheltemai new species
Figures 16–21 + 28

Holotype: MCZ 279905. (Type locality: ATLANTIS II, Cruise 60, Station 242, Argentine Basin, Lat. 38°16.9'S, Long. 51°56.1'W, in 4382–4405 m.)
Records: Argentine and Guiana Basins. Depth range = 3305–4405 m.

Specific Description. Shell inequilateral, laterally compressed, obliquely oblong/oval in outline, with strong, even concentric lines; rostrum well developed and sharply pointed; umbos anterior and low in profile, very small in larger specimens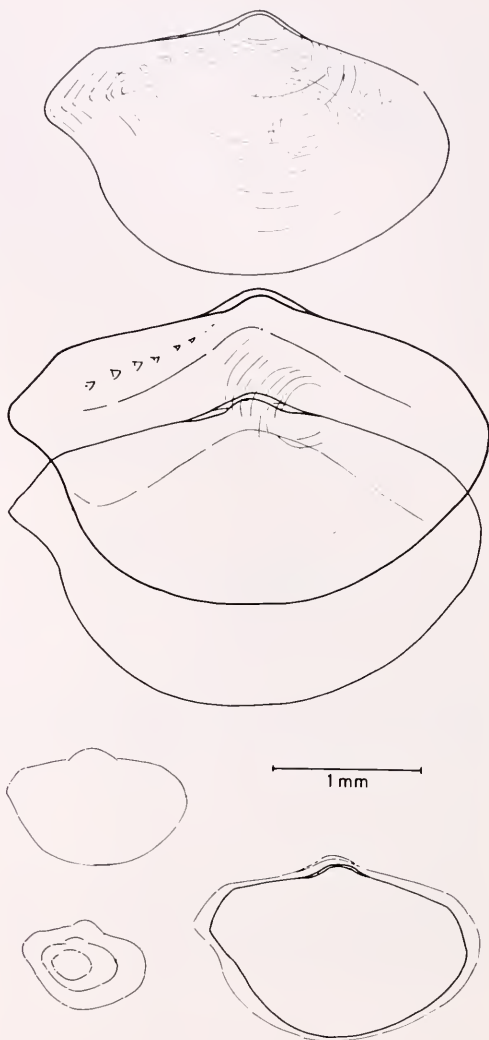, more posterior and relatively larg-er in small specimens, beaks medially directed; except distally, dorsal margin long and relatively straight; antero-dorsal margin slightly convex to about the level of 12th tooth, thereafter sloping abruptly and ventrally to form smooth curve with anterior margin; postero-dorsal margin straight, to level of 10th tooth where it becomes markedly concave, forming the
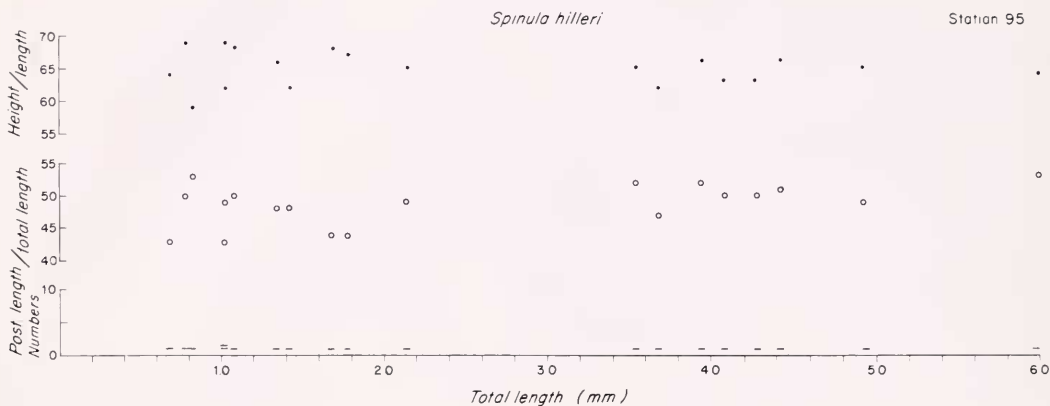
Figure 15. *Spinula hilleri.* Changing shell shape with increasing size as measured by the ratios of height/total length and posterior shell length (umbo-rostrum)/total length to total length.

dorsal side of sharp rostrum; rostrum ventrally concave, remainder of posterior margin broadly truncate; ventral margin long and, except anteriorly, only slightly convex; maximum height of shell well posterior of umbo; well-developed keel close to postero-dorsal margin, less evident near umbo and extending to tip of rostrum, concentric lines making a sharp right angle at keel; hinge plate long and shallow, anterior and posterior plates relatively straight, diverging from dorsal shell margin, anterior hinge plate with 15 small chevron-shaped teeth, posterior plate with 14 small teeth, proximal teeth

minute, distal teeth relatively small; ligament amphidetic, inner layer (resilium) wide and lunate, outer layer and periostracum elongate with posterior part slightly longer than anterior and extending beyond posterior hinge plate, anterior part extending to level of 11th tooth. Maximum recorded shell length 11.5 mm.

The present species might superficially be confused with *Spinula oceanica*, which has a somewhat similar shell outline. However, *Spinula oceanica* differs in sculpture, and the anterior dorsal shell margin slopes sharply ventrally immedi-

TABLE 5. RECORDS FOR *Spinula scheltemai* NEW SPECIES.

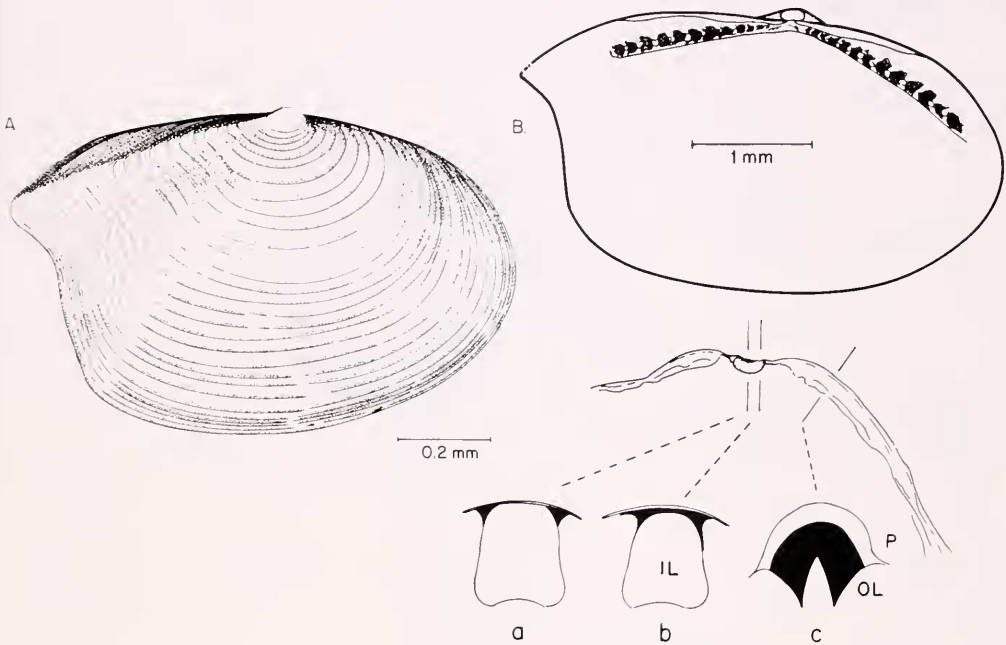| Cruise	No.	Station no.	Depth (m)	No. of specimens	Latitude	Longitude	Gear	Date
				Argentine Basin				
ATLANTIS II	60	259A	3305–3317	5	37°13.3′S	52°45.0′W	ES	26.3.71
ATLANTIS II	60	256	3906–3917	230	37°40.9′S	52°19.3′W	ES	24.3.71
ATLANTIS II	60	242	4382–4405	68	38°16.9′S	51°56.1′W	ES	13.3.71
				Guiana Basin				
KNORR	25	307	3802–3825	10	12°34.4′–12°40.8′N	58°59.3′–59°09.2′W	ES	3.3.72

Figure 16. *Spinula scheltemai*. A. External view of right valve of holotype (MCZ 279905) from Station 242. B. Internal view of a left valve from the same station and lateral view of the ligament removed from the hinge plate. a, b, and c, transverse sections through the internal ligament (resilium) and external ligament at the points indicated by the broken lines. *Abbreviations:* P, periostracal layer; IL, inner layer; OL, outer layer.

ately anterior to the umbo. The hinge plate is more slender in *S. oceanica* with the teeth even closer to the dorsal margin. The external ligament is at least twice as long in *S. scheltemai* as in *S. oceanica* and larger than in any other species recorded here.

We name this species after our friend and colleague Dr. Rudolf Scheltema of the Woods Hole Oceanographic Institution.

Morphology. Although the form of the body and mantle is similar to that of other species, the body of *S. scheltemai* occupies more shell space than any other species (Fig. 17). The adductor muscles are much closer to the shell margin, particularly the posterior, possibly because the rostrum of *S. scheltemai* is not greatly extended. The adductor muscles are very large, while the siphonal embayment is short. The anterior sense organ is far anterior in position, but because the adductor muscle lies close to the shell margin, the sense organ is situated immediately below the muscle.

The palps are relatively much larger than in the other species described here. Depending on the size of the animal, 26–50 ridges are present, the palps extending across the entire width of the body. The palp proboscides are very short in the preserved specimens and fill the space between the ventral edge of the gill and the posterior edge of the palp. The gills are moderately well developed with about 25 gill plates to each demibranch. The ganglia are large. A siphonal tentacle inserts either on the left or right side of the base of the siphon. The siphon is moderately large. The gills are attached laterally to the base of the siphon
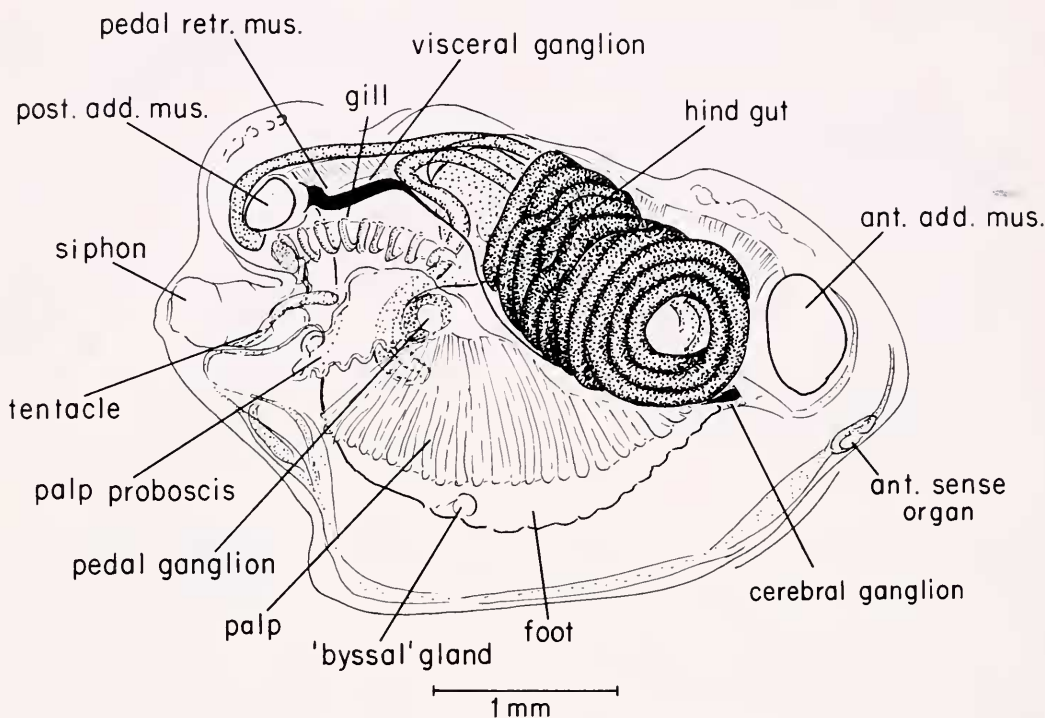
Figure 17. *Spinula scheltemai.* Semidiagrammatic view of the right side of animal to show disposition of organs.

(Fig. 19). The siphon is not obviously a double structure of the type figured by Yonge (1939). It is internally ridged. The mid-lateral ridges, continuations of the gill attachment, are somewhat more obvious than the others. Faecal rods are confined to the dorsal side of the lumen, and probably the internal ridging effectively divides the siphon in two. Dorsally, the siphon is attached by connective tissue that passes postero-lateral to the hind gut.

The gut takes the usual course. Here the mid gut and hind gut penetrate some distance into the foot ventral to the large pedal ganglia. There are 10 coils on the right side of the body, although in most specimens there appear to be only 8. However, sections and whole mounts show that two of the coils may be hidden internal to the tightly packed outer coils. The stomach is large and displaced far to the left side of the body (Fig. 18).

The foot and the 'byssal' gland are well developed. The pedal retractor muscles are similar to those described for *S. filatovae* (p. 7).

There is a change in shape with increasing length (Fig. 20). As in other species, increasing prominence of the rostrum results in a change in position of the umbo relative to the total length. In some cases (Fig. 21) the umbo is posterior to the midline. Total length with respect to height changes but little during the growth of the animals. The smallest specimen showing gonadal development was 2.4 mm total length. Sexes are separate with the larger animals tending to be more mature. No specimen appeared to
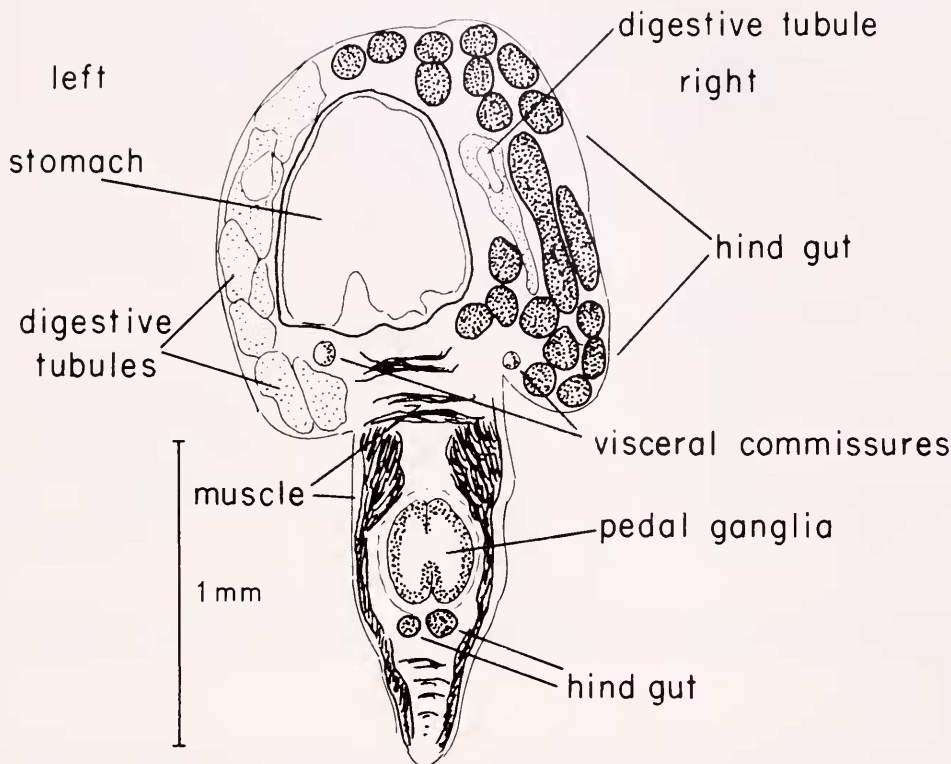
Figure 18.   *Spinula scheltemai.* Transverse section through viscera and foot to show position of hind gut and stomach. Pedal ganglia also present with distal end of style sac and proximal end of hind gut in section.

be fully mature. The larval shell measures about 375 μm—the smallest recorded for an Atlantic *Spinula*.

Spinula subexcisa (Dautzenberg and Fischer, 1897)
Figures 22–28

Leda excisa var. *subexcisa* (Dautzenberg and Fischer, 1897: 205. (Type locality: Azores, PRINCESSE-ALICE, Station 69, in 1846 m; type specimen supposedly housed in Institut Oceanographique, Monaco, present whereabouts unknown.)
Previous records (see p. 2): Throughout Atlantic, 1848–5153 m. Probably many previous records have been confused with other species described in this paper. The Norwegian and W. European records can be accepted with some degree of certainty.
Present record: West Europe Basin, 1993 m.

Historical. The first record of *S. subexcisa* was almost certainly that described by Jeffreys (1876, 1879) and incorrectly referred to as *Malletia excisa* (Philippi). The specimens examined by Jeffreys were taken by the PORCUPINE and LIGHTNING expeditions from a position very close to that of the present records for *S. subexcisa*. Jeffreys (1876, 1879), like ourselves, only recognized one species from the area. Jeffreys regarded his specimens as being recent examples of the Sicilian fossil *Nucula excisa* Philippi (1844). As a result he did not figure his specimens, nor did he give a sufficiently accurate description of the specimen to confirm its specific identity. Smith (1885), who identified a specimen as being the same species as that de-
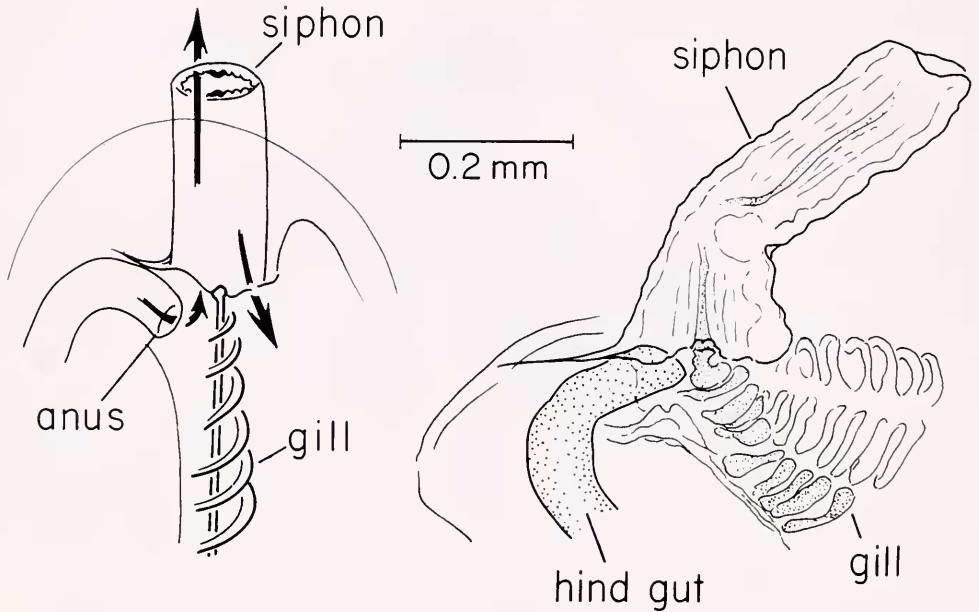
Figure 19. *Spinula scheltemai.* Detail of siphonal region, with diagram to show route of faeces and path of incoming inhalent flow.

scribed by Jeffreys (1876, 1879), reported that its sinus was not as deep as that figured by Philippi (1844). Unfortunately, this unfigured CHALLENGER specimen from the Azores is equally likely to have been a specimen of *S. hilleri* and not *S. subexcisa.* Dautzenberg and Fischer (1897) also came to a conclusion similar to that of Smith (1885) and named their specimens from off the Azores as *Leda excisa* var. *subexcisa.* They gave a somewhat more adequate specific description.

Although we have been unable to examine the specimens referred to above, we have little doubt that our specimens, from almost the same locality where only a single species of *Spinula* is recorded, are the same species that Jeffreys (1876, 1879) examined from the PORCUPINE and LIGHTNING material. Furthermore, the present specimens are certainly not *Leda excisa* (Philippi, 1844), being a totally different shape. They do, however, agree closely with the description of Dautzenberg and Fischer (1897).

Because of the uncertainties in previous descriptions and because the animal itself is not described, we redescribe the species in some detail.

Specific Description. Shell moderately strong, concentric sculpturing somewhat

TABLE 6.   RECORD FOR *Spinula subexcisa* (DAUTZENBERG AND FISCHER).

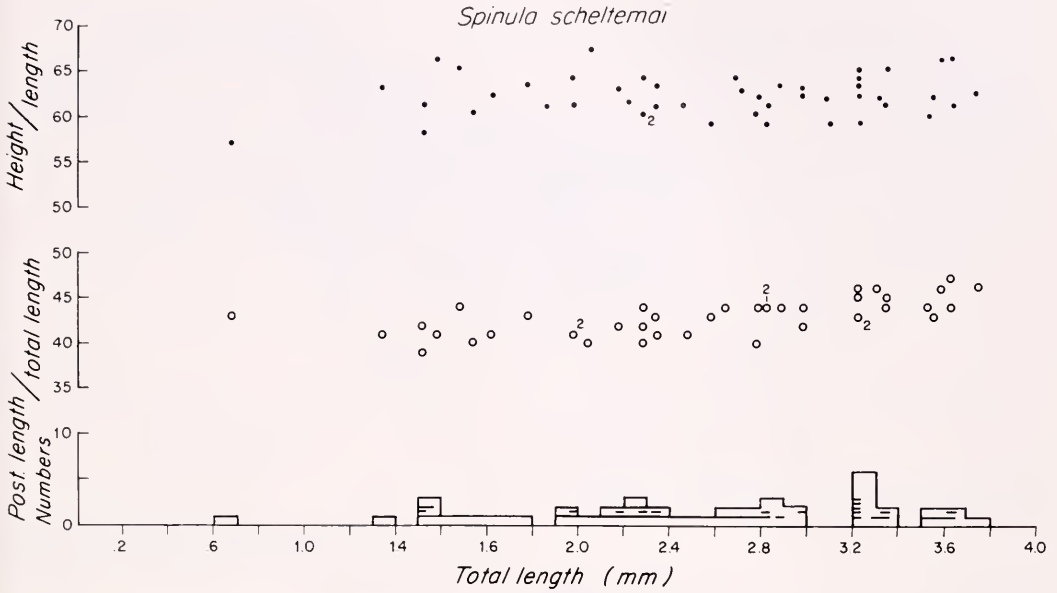| Cruise	No.	Station no.	Depth (m)	No. of specimens	Latitude	Longitude	Gear	Date
West Europe Basin								
CHALLENGER		4	1993	88	56°52.0′N	10°01.0′W	ES	5.6.73

Figure 20. *Spinula scheltemai*. Changing shell shape with increasing size ratios of height/total length and posterior shell length (umbo-rostrum)/total length to total length.

variable both in sharpness of line and in interval; rostrum moderately long and sharply pointed; umbos large, slightly anterior in older specimens, beaks medially curved; dorsal margin sloping gently from the umbo; antero-dorsal margin very slightly convex and forming a smooth curve with anterior margin; postero-dorsal margin very slightly concave to a point immediately posterior to hinge plate where it makes an angle to form the convex dorsal edge of the rostrum, ventral edge of rostrum concave; ventral margin a smooth curve, more convex posteriorly than anteriorly, rostral keel not marked; hinge plate moderately broad distally but coming close to shell margin below umbo, ventral edge of both anterior and posterior hinge plates almost straight; number of teeth varies with size of animal, in largest specimens 11 anterior and 10 posterior teeth—the 6 distal teeth much larger than the rest, those nearest umbo very difficult to distinguish; ligament amphidetic, inner layer
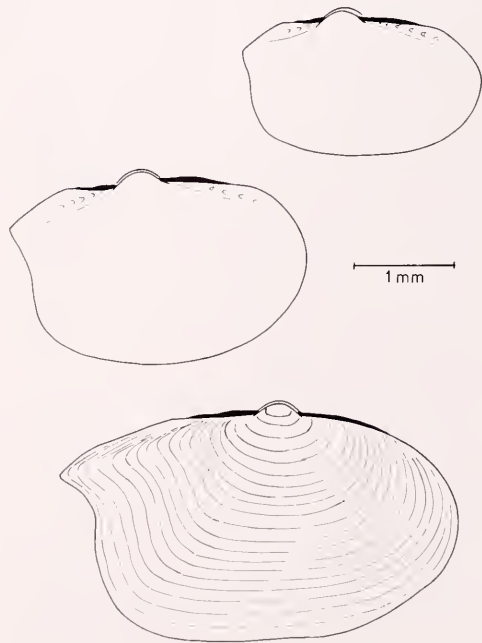

Figure 21. *Spinula scheltemai*. Lateral views of a series of specimens to show change in shell outline with increasing size.
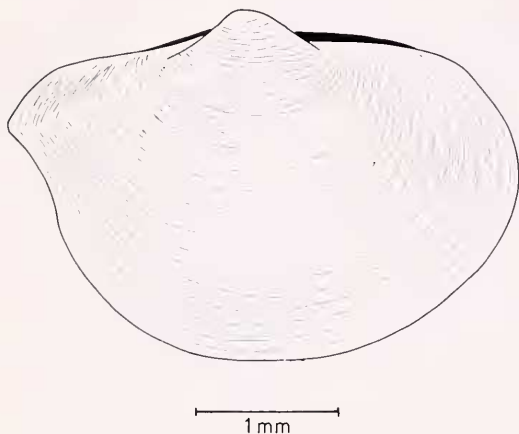
Figure 22.   *Spinula subexcisa.* Lateral view of a specimen to show external features of the shell.

Figure 23.   *Spinula subexcisa.* Lateral view of the right and left valves of two different specimens to show shell outline, hinge plate, and differences in tooth number with increasing size of shell.

(resilium) relatively large, oval, occupying width of hinge below umbo, outer layer external and elongate, extending to level of the eighth anterior tooth and seventh posterior tooth in largest specimens. Maximum recorded shell length 4.4 mm.

Spinula subexcisa is very similar in general shape to *S. scheltemai*, but it can be distinguished from the latter species by the smaller number of teeth, the breadth of the hinge plate, the length of the posterior outer layer of the ligament and the less regular, but more closely spaced, concentric sculpture (Figs. 22, 23).

Morphology. The basic form of the body is identical to the other species described here (Fig. 24).

The adductor muscles are unequal in size, the anterior being approximately four times as large as the posterior. The 'quick' and 'catch' sections are clearly visible. The anterior sense organ is far anterior, below but in front of the anterior adductor muscle. The sense organ is particularly well developed, being a semicircular flap of tissue that is an extension of the middle sensory lobe. Underlying the epithelium in this region (both lining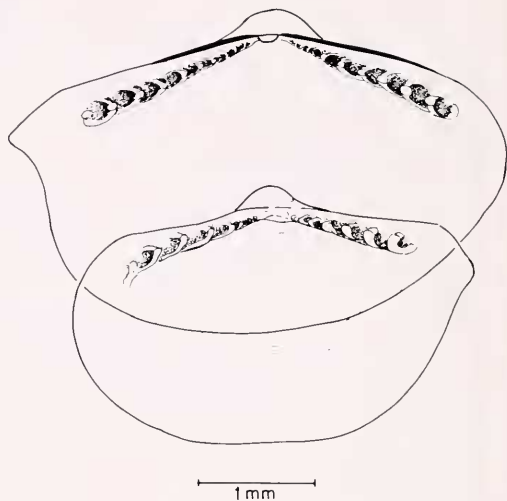 the shell and the mantle cavity) is a thick layer of connective tissue with an enlarged space containing the pallial nerve (Fig. 25). The area is also well supplied with glandular epithelial cells, with one well marked dome-shaped patch at the anterior limit of the organ.

The siphon and the feeding aperture are similar to those of other species of *Spinula*. The sensory tentacle lies on the left side at the base of the siphon in most specimens stained as whole mounts.

The palps, with at least 32 narrow ridges, are large and extend the width of the body. The palp proboscides are small and in their contracted state lie between the gill and the posterior rim of the palp. There are 12–18 gill plates in each demibranch; like the palp ridges, the number is dependent on the size of the specimen. As in *S. scheltemai*, the body and foot occupy much of the mantle space. The posterior margin of the foot is extended posteriorly and lies close to the feeding aperture.

As in all species, the mouth is displaced a short distance posterior to the anterior adductor muscle. The course of
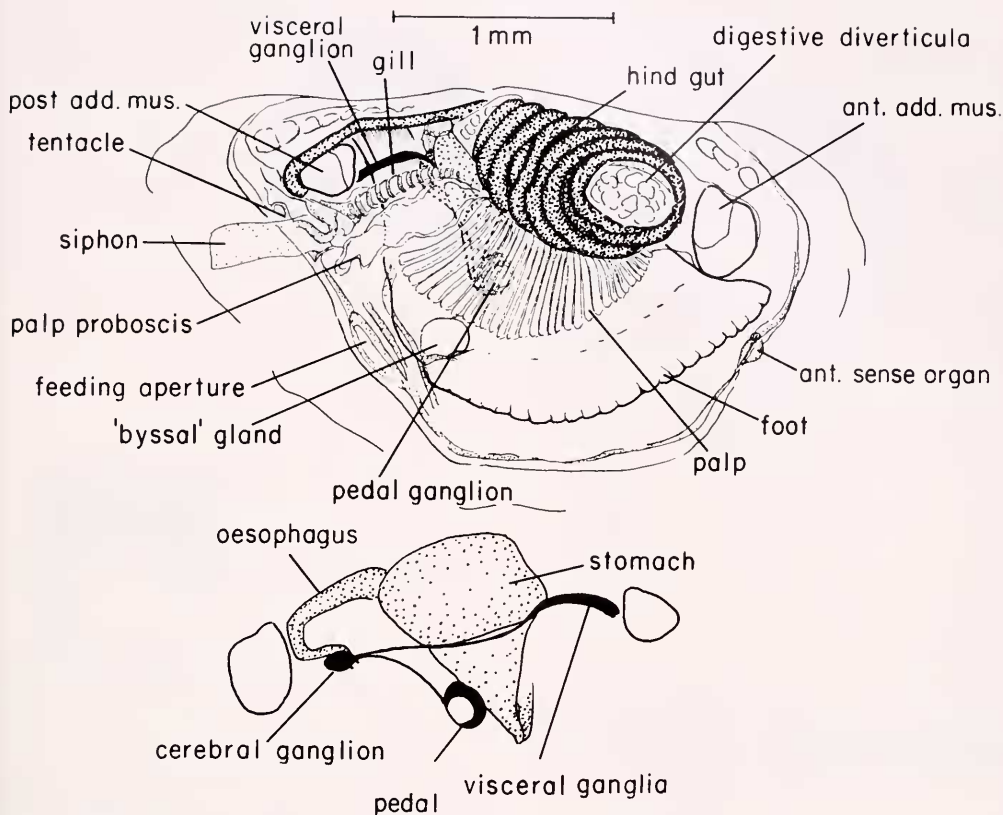
Figure 24. *Spinula subexcisa.* Semidiagrammatic view of right side of the animal to show disposition of organs. Below is detail of stomach and ganglia of the same specimen, but drawn from the left side.

the oesophagus is initially anterior as far as the posterior face of the muscle where it turns posteriorly to join the stomach. The stomach lies posterior and dorsal within the body and is displaced to the left side. On the right there are nine coils of the hind gut. The ganglia are well developed, particularly the pedal, which lies posterior and relatively high in the foot. The foot is not as markedly anterior in its attitude as it is in the more elongate species. The 'byssal' gland is spherical and lies close to the margin of the foot (Fig. 26). The peripheral muscles of the foot form a network around the gland, and appear to form a sphincter at the neck of the gland. The gland itself is composed of hyaline cells. Its function is obscure.

As in other protobranchs, no byssus is produced, nor does the gland bear any similarity to the lamellibranch byssus apparatus.

The larval shell measures 450 μm, the largest for an Atlantic species. The juveniles are much more angular than the adults, with rostrum, posterior margin, and antero-dorsal margin combining to give a somewhat elongate, hexagonal appearance (Fig. 27). As growth proceeds, the posterior margin becomes sinusoidal, the rostrum more pronounced, and the anterior margin more rounded.

DISTRIBUTION PATTERNS

Of the five species of *Spinula* recorded from the Atlantic, three species, *S. hil-*
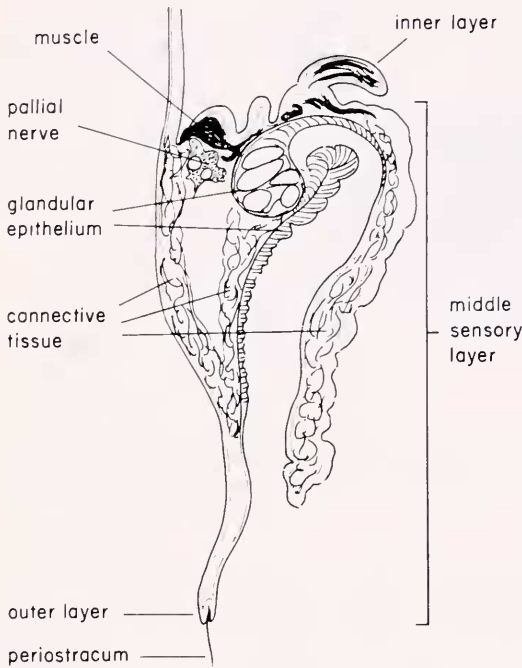
Figure 25. *Spinula subexcisa.* Diagrammatic view of mantle margin cut transversely through the anterior part of the anterior sense organ.
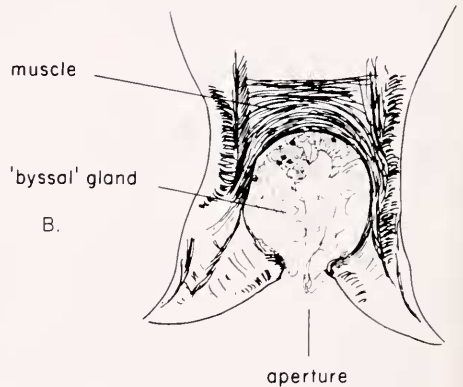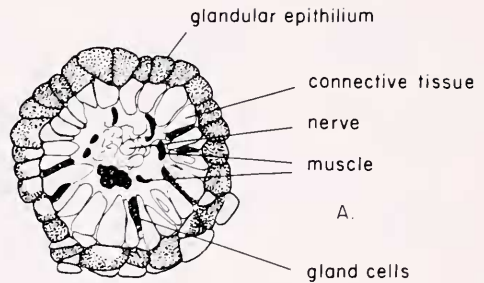

Figure 26. *Spinula subexcisa.* A. Transverse section through sensory tentacle. B. Transverse section through 'byssal' gland and foot musculature.

leri, S. scheltemai, and the unnamed species, live in abyssal depths (2500–5000 m), while *S. filatovae* is present at lower slope depths (1200–1800 m), and *S. subexcisa* is probably found on the lower slope and upper abyssal rise (1800–2500 m).

All species, except *S. hilleri,* have somewhat restricted distributions. *S. hilleri* is found in the West Europe, Canary, Cape Verde, Brazil, Angola, and Argentine Basins. It is moderately abundant, numerically forming more than 10% of the protobranch fauna in 3 of the 17 stations where it was found. *Spinula scheltemai* is present in the Argentine and Guiana Basins. In the former basin, it is numerically abundant, forming more than 10% of the protobranchs in two of the three samples that contained it. *S. subexcisa* has been found only in the

West Europe Basin where it is a common faunal constituent. In contrast, the unnamed species limited in our samples to the North America Basin, is a rare species. We have collected but a single individual in each of three samples, yet this is one of the most extensively sampled deep-sea basins.

The slope-dwelling species, *S. filatovae,* occurs in the northeastern Atlantic and was present at single stations in the West Europe and Cape Verde Basins, numerically comprising 5% and 6% respectively of the protobranchs in these samples. It occurs at similar depths in the Guinea Basin. Curiously, it is the only species of those described here that, to date, has been recorded outside the At-
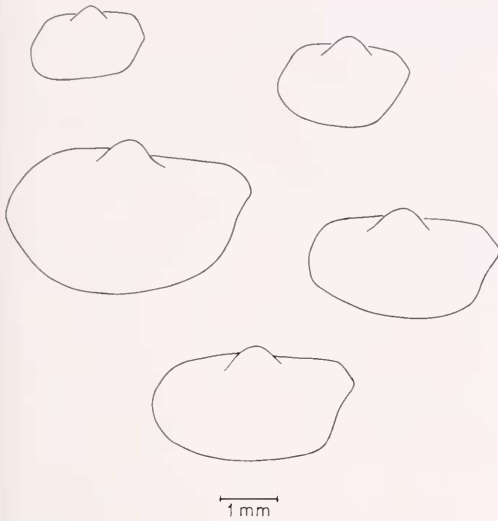
Figure 27. *Spinula subexcisa*. Series of shell outlines in lateral view to show change in shape with increasing size.
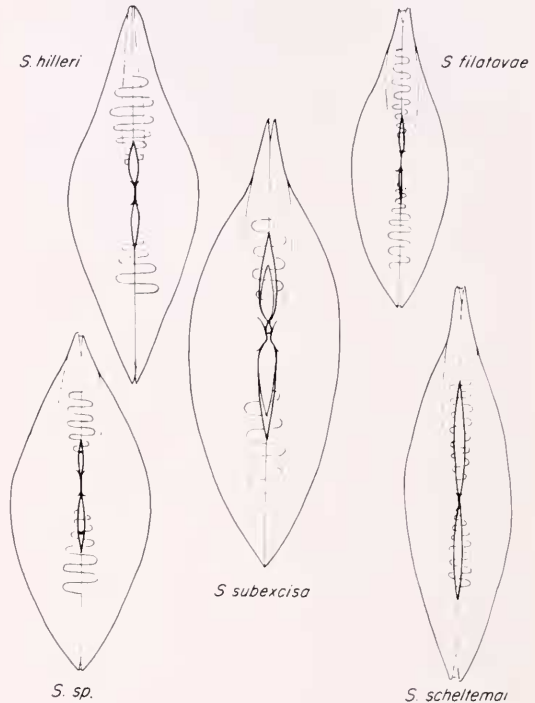

Figure 28. Dorsal view of shell of the five species of *Spinula* from the Atlantic to show differences in shell shape and extent of external ligament.

lantic—a single record from the Gulf of Aden (Knudsen, 1967). Thus, *S. filatovae* may occur along the lower slope of the eastern mid and South Atlantic and extend around the Cape of Good Hope into the western Indian Ocean. Yet, the remarkable differences in the depth records for this species in the Atlantic (1261, 1376, 1624–1796, and 1739 m) as compared to the Indian Ocean and Gulf of Aden (2312, 3152–3202, 3546, 4300–4340, and 4314–4324 m), together with the absence of any detailed knowledge of the soft part anatomy for the Indian Ocean specimens, raise the possibility that we may unwittingly be lumping together two morphologically similar species. *S. filatovae* appears to be absent from the western Atlantic.

MORPHOLOGICAL CONSIDERATIONS

Both the shell and soft parts of species in the genus *Spinula* are amazingly conservative. Of the species recorded from the Atlantic, specific shell differences are a matter of subtle variations in shape and dimension. At one extreme there is a bivalve with a robust broad hinge with heavy teeth (Figs. 11, 28) combined with small adductors (Fig. 12) and a relatively short amphidetic ligament without a strongly developed outer layer (Fig. 28). At the other extreme there is a bivalve with a less robust, slimmer hinge with finer, more numerous teeth (Fig. 16), large adductors (Fig. 17), and a well-developed elongate, arched outer layer to the ligament (Fig. 28). The latter type of ligament is reminiscent of the external ligament (albeit opisthodetic) of the Tellinacea. Possibly the analogy can be stretched further to suggest that *Spinula* is the deep-sea, deposit feeding, counterpart of *Tellina*, a slender, active deep burrowing, deposit feeder.

This view is reinforced by various points of morphology. *Spinula* is well endowed with large ganglia, particularly the pedal; the foot is very elongate and

muscular, somewhat anteriorly directed, particularly in the elongate species, and the viscera do not penetrate it to any great degree; the siphon is long and muscular; the adductor muscles, although unequal, are powerful with clearly defined 'quick' and 'catch' parts; and the anterior sense organ is far anterior. All these features suggest that *Spinula* is an active burrowing infaunal bivalve.

Other characteristics typical of deep-sea genera (Allen, 1975) are the large, finely-ridged palps and the relatively small gills with few gill plates. *Spinula filatovae*, the slope species, has the largest number of gill plates and the smallest palp with relatively few palp ridges. *Spinula hilleri, S. scheltemai, S. subexcisa,* and the unnamed species are remarkably alike with respect to gill and palp morphology. Similarly, in *S. filatovae* the hind gut, although much coiled, is relatively small in diameter, the coils being mostly laid on top of one another, while in the other four species the coils tend to be overlapping and with a much wider lumen. The number of coils varies: *S. filatovae* (6), the unnamed species (7), *S. subexcisa* and *S. hilleri* (9), and *S. scheltemai* (10), with occasional variation within species. Increase in gut volume and length with increasing depth is well known in bivalves. Although not so well defined in terms of increasing number of coils with increasing depth distribution, this principle still holds in general terms for the genus *Spinula*. The Pacific species *S. tasmanica* (6), *S. vityazi* (7), and *S. kermadecensis* (7) possibly have fewer coils, but further investigations might show additional hidden coils beneath those closely packed coils at the surface. The exception to the general rule of a multiple-coiled hind gut on the right side of the body is *Spinula calcar* (4063–6096 m) (Dall, 1908). It has one hind gut loop on the right side of the body, which is the primitive condition in protobranch bivalves. It seems that the morphology

and taxonomy of this species should be re-examined.

Spinula is clearly adapted to deal with large quantities of sediment entering the mantle cavity. Judging from the extension of the posterior margin of the foot, unwanted sediment is thrust out of the feeding aperture by the heel. It is possible that the 'byssal' gland secretes an adhesive fluid to bind unwanted particles together before they are rejected. It is strategically placed and of a large enough size in *Spinula* to perform this function. In addition, there are large numbers of mucous glands present in the region of the feeding aperture. However, these may be more concerned with the processing of incoming particles on the palp proboscides than with outgoing pseudofaeces.

The unequal size of the adductor muscles, *not* associated here with anterior enlargement of the mantle cavity, may serve to prevent the combined siphon, on the occasion of its retraction, from being trapped by the closing valves. It may also serve to assist in clearing large quantities of pseudofaecal material. Certainly, large amounts of sediment are present in the posterior part of the mantle cavity of many specimens. However, the very nature of the methods of collection prevents any emphatic and significant conclusion from being drawn.

The sediment in the gut is very fine and, for the most part, is composed of fragments of diatoms and foraminiferans. It is difficult to say whether these fragments are in any way concentrated or selected.

Although the larval shell indicates a large egg, there is no evidence of direct development. For the most part, our samples show either immature or only partially mature animals. Sexes are separate. The most mature animals are among the largest, and the picture presented is similar to the one seen in the case of *Tindaria*. Whether or not *Spinula*, like the

latter genus, is long-lived (Turekian *et al.*, 1975) will have to await dating by ra-dio-chemical methods.

ACKNOWLEDGMENTS

LITERATURE CITED

ALLEN, J. A. 1975. The adaptations of the bivalves of the Atlantic abyssal plain. Proc. Challenger Soc., **4**: 248–251.

ALLEN, J. A., AND H. L. SANDERS. 1969. *Nucinella serrei* Lamy (Bivalvia: Protobranchia), a mono-myarian solemyid and possible living actino-dont. Malacologia, **7**: 381–396.

———. 1973. Studies on Deep-Sea Protobranchia (Bivalvia); The families Siliculidae and Lame-tilidae. Bull. Mus. Comp. Zool., **145**: 263–310.

ALLEN, J. A., AND J. F. TURNER. 1974. On the func-tional morphology of the family Verticordiidae (Bivalvia) with descriptions of new species from the abyssal Atlantic. Phil. Trans. Roy. Soc. Lond., B, **268**: 401–536.

BELYAEV, G. M. 1966. Hadal bottom fauna of the world ocean. Moscow, Institute of Oceanology, Academy of Sciences of the USSR, 199 pp.

CLARKE, A. H. 1962. Annotated list and bibliog-raphy of the abyssal marine molluscs of the world. Bull. Natn. Mus. Can., **181**: 1–114.

DALL, W. H. 1908. The Mollusca and the Brachi-opoda. Reports on dredging operations off the West Coast of Central America by the U.S. Fish Commission steamer 'Albatross.' Bull. Mus. Comp. Zool., **43**: 205–487.

DAUTZENBERG, P. 1889. Contribution à la faune malacologique des iles Azores. Rèsult. Camp. Scient. Prince Albert I, **1**: 1–112.

———. 1927. Mollusques provenant des compagnes scientifiques du Prince Albert 1er de Monaco dans l'Ocean Atlantique et dans le Golfe de Gascogne. Rèsult. Camp. Scient. Prince Albert I, **72**: 1–400.

DAUTZENBERG, P., AND H. FISCHER. 1897. Dra-gages effectives par l'Hirondelle et par le Prin-cesse-Alice 1888–1896. Mem. Soc. Zool. Fr., **10**: 139–234.

FILATOVA, Z. A. 1958. On some new species of bivalve molluscs from the North-Western part of the Pacific Ocean. Trudy Inst. Okeanol., **27**: 208–218. (In Russian.)

———. 1964. A new species of bivalve molluscs from the ultra-abyssal of the Pacific. Zool. Zh., **43**: 1866–1868. (In Russian.)

———. 1976. Composition of the genus *Spinula* (Dall, 1908), family Malletidae and its distri-bution in the ocean. Deep-sea bottom fauna of the Pacific Ocean. Proc. P. P. Shirshov Inst. Oceanol., **99**: 219–240. (In Russian.)

HERTLEIN, L. G., AND A. M. STRONG. 1940. Mol-lusks from the west coast of Mexico and Cen-tral America. Eastern Pacific Expeditions of the New York Zoological Society XXII. Zool. N.Y., **25**: 369–430.

JEFFREYS, J. G. 1876. Preliminary report of the biological results of a cruise in H.M.S. "Valor-ous" in Davis Strait 1875. Proc. Roy. Soc. Lond., **25**: 177–230.

———. 1879. On the Mollusca procured during the "Lightning" and "Porcupine" Expeditions, 1869–1879. Part II. Proc. Zool. Soc. Lond., 1879, pp. 553–588.

KNUDSEN, J. 1967. The deep sea Bivalvia. Scient. Rep. John Murray Exped., **11**: 237–343.

———. 1970. The systematics and biology of abys-sal and hadal Bivalvia. Galathea Rep., **11**: 7–241.

LOCARD, A. 1898. Mollusques Testaces 2. Expéd. Scient. Trav. Talisman, pp. 1–515.

OKUTANI, T. 1974. Review and new records of abyssal and hadal molluscan fauna in Japanese and adjacent waters. Venus, **33**: 23–39.

———. 1975. Deep sea bivalves and scaphopods collected from deeper than 2000 m in the North Western Pacific by R/V Soyo-Maru and the R/V Kaigo/Maru during the years 1969–1974. Bull. Tokai Reg. Fish. Res. Lab., No. 82, pp. 57–87.

PHILIPPI, R. A. 1844. Enumeratio Molluscorum Siciliae cum viventium, tum in tellure tertiaria fossilium quae in iternere suo observavit. 2. Naples, pp. 45–48.

SANDERS, H. L., AND J. A. ALLEN. 1973. Studies on Deep-Sea Protobranchia (Bivalvia); Prologue and the Pristiglomidae. Bull. Mus. Comp. Zool., **145**: 237–262.

———. 1977. Studies on the Deep Sea Protobran-

chia (Bivalvia); The family Tindariidae and the Genus *Pseudotindaria*. Bull. Mus. Comp. Zool., **148:** 23–59.

SMITH, E. A. 1885. Report on the Lamellibranchia collected by H.M.S. 'Challenger' during the years 1873–76. Rep. Scient. Res. Challenger, **13:** 1–341.

SUYEHIRO, Y., Y. OKADA, M. HORIKOSHI, AND E. IWAI. 1962. A brief note on the benthic animals on the fourth cruise of the Japanese Expedition of Deep-Seas (J. EDS-4). Oceanogr. Mag., **13:** 149–153.

TUREKIAN, K. K., J. K. COCHRAN, D. P. KHARKAR, R. M. CERRATO, H. L. SANDERS, J. F. GRASSLE, AND J. A. ALLEN. 1975. Slow growth rate of a deep-sea clam determined by ^{228}Ra chronology. Proc. Nat. Acad. Sci., **72:** 2829–2832.

WOLFF, T. 1960. The hadal community, an introduction. Deep-Sea Res., **6:** 95–124.

YONGE, C. M. 1939. The protobranchiate Mollusca; a functional interpretation of their structure and evolution. Phil. Trans. Roy. Soc. Lond., B, **230:** 79–147.